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Relationships between feeding behaviour, activity, dominance and feed efficiency in
finishing beef steers

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27 Abstract

28 To increase the profitability and sustainability of beef production systems, the
29 use of animals with high feed efficiency is preferred. Efficient animals eat less than
30 their peers for the same or better growth. This efficiency can be measured using feed
31 conversion ratios (FCR) and residual feed intake (RFI) parameters. However, the
32 biological mechanisms, particularly those related to the animal's behaviour and
33 personality, are poorly understood. An individual animal's behaviour, such as its
34 activity levels, may contribute to efficiency. Feed intake is also a factor in efficiency,
35 and therefore, social dominance rank may also indirectly affect efficiency through its
36 influence on feeding behaviour. This experiment investigated the effects of dominance
37 on feeding behaviour, as well as of dominance and activity on average daily gain
38 (ADG), FCR and RFI in two breeds of beef cattle. The study used a 2 x 2 design with
39 80 cattle of two breed-types (Charolais-cross (CHx) (n=41) and Luing (n=39)) and two
40 diets (a concentrate-based diet (CONC) and a mixed forage and concentrate diet
41 (MIXED)). For each individual steer, FCR and RFI were measured over a 56-day
42 performance test. Feed intake, patterns of feeding behaviour, activity and dominance
43 were also measured. Feed intake was affected by dominance, with more dominant
44 steers having significantly higher dry matter intakes ($P=0.001$) and feeding rates
45 ($P=0.006$) suggesting that dominant animals had priority of access to the feeders.
46 Steers with higher ADG had higher intakes and performed more standing bouts. Steers
47 with better FCR values performed more standing bouts and younger animals had better
48 FCR. For RFI there was also an interaction between breed and variation in length of
49 the feeding events, showing that Luing steers with more consistent feed bout lengths
50 had better RFI, with no association shown for CHx steers. There was no direct effect of

51 dominance on ADG, FCR or RFI. However, the effect of dominance on feed intake
52 suggests that measures of performance in any study may be affected by feeder-space
53 allocation. The associations between standing bouts and feeding bouts with efficiency
54 measures also suggest that individual animal behavioural characteristics influence
55 efficiency and that overall efficiency of all animals may be improved by allowing
56 animals to express individual patterns of behaviour.

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58 Key words: activity, dominance, efficiency, beef cattle, feeding behaviour

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1. Introduction

Increasing the production outputs or growth of animals for a fixed amount of feed is seen as a means of reducing costs and improving profitability in beef production systems (Archer et al., 1999; Arthur et al., 2004). The term ‘feed efficiency’ is used to describe the relationship between feed inputs and growth outputs, with efficient animals being those that grow well but consume less feed compared to others in their cohort. As well as improving farm profitability, increasing feed efficiency is an important means of reducing the environmental impact associated with beef production. Ruminants are responsible for an important proportion (between 6-8-%) of the global anthropogenic methane emissions (Gerber et al., 2013).

A great deal of research has focussed on achieving improvements in feed efficiency in beef production systems worldwide (e.g. Archer et al., 1999; Arthur et al., 2004; Basarab et al., 2003). A number of measures have been developed to quantify feed efficiency. Feed conversion ratio (FCR) measures the amount of feed required per unit of growth (e.g. Archer et al., 1999; Robinson and Oddy, 2004), while residual feed intake (RFI) is the difference between an animal’s actual feed intake and its expected intake requirements for growth and maintenance estimated using others in its cohort in a given production system (Archer et al., 1999; Koch et al., 1963). Thus an animal that eats less than expected over the test period will be more efficient and have a negative RFI value (Richardson et al., 2002).

Given the link to productivity, it is not surprising that research into feed efficiency has most entirely focussed on animal-level factors affecting productivity, such as breed and diet (e.g. Basarab et al., 2003; Golden et al., 2008), but little is known about the underlying biological causal factors, such as behaviour or physiology. In a review of the subject, Herd et al. (2004) suggested that there were a number of factors that may

contribute to individual differences in efficiency including activity, feed intake and digestion, metabolism and thermoregulation. Studies have investigated the relationship between overall activity and RFI. A study by Richardson et al. (2000) has shown that inefficient animals with high RFI scores took a greater number of steps per day than animals with better efficiency. A higher step-count in steers with poor RFI scores has also recently been confirmed by Llonch et al., (in press), but has not been shown in a number of other studies with beef cattle (e.g. Hafla et al., 2013; Lawrence et al., 2011). Higher activity has also been associated with poor efficiency in other species (Luiting et al., 1994).

The direct relationship between feeding behaviour and efficiency has already been investigated in a number of studies. The results suggest that efficient animals (those with low RFI scores) have a shorter duration of feeding each day (Basarag et al., 2007; Durunna et al., 2011; Lancaster et al 2009; Nkrumah et al., 2007) and fewer feeding events per day (Durunna et al., 2011; Golden et al, 2008; Kelly et al., 2010; Lancaster et al 2009; Nkrumah et al., 2007). Steers with a higher frequency of feeding events had lower (more favourable) FCR values (Nkrumah et al., 2007).

However, other behavioural traits may also be important, particularly those that can affect feed intake and feeding behaviour. The social dominance rank of the animal is known to affect feeding behaviour. High social dominance rank generally infers priority of access to resources (Syme, 1974) which includes access to food (e.g. McPhee et al., 1964). In dairy cattle, it has been shown that in situations where there is limited access to feed, animals of low dominance rank or younger animals can be displaced from the feeder by higher-ranking animals (Gibbons et al., 2009; Huzzey et al., 2006). Low-ranking animals may also avoid approaching feeders when dominant animals are present. Both of these factors will affect feeding frequency and duration.

Fewer studies have been carried out in beef cattle, but they also suggest that dominance affects access to feed (Stricklin and Gonyou, 1981; Llonch et al., in press).

The hypothesis that dominance may affect feeding behaviour in beef cattle has relevance for the assessment of feed efficiency. Typically, feed efficiency trials are carried out using automatic feed bins that record the amount of feed consumed by each animal. However, the number of bins provided is normally lower than the number of animals, which may create a situation of competition. For instance, Golden et al (2008) had 1 bin to every 3 animals, while Fitzsimmons et al., (2014) had 1 bin per eight to nine animals. Thus, in these situations, dominance rank may influence feed intake and patterns of feeding behaviour, which may have an indirect affect on the individual animal's ability to express its full potential for efficiency.

The first hypothesis of this study is that dominance will affect feed intake in a typical feed efficiency trial in which there are fewer automatic feeders than there are animals. Secondly, we hypothesis that dominance, activity and feeding behaviour affect efficiency.

2. Materials and Methods

The behavioural data were taken as part of an overall trial that investigated the growth, efficiency and methane emissions of two breed types of beef cattle on two types of diet. The experiment was of a 2 x 2 factorial design, with 2 breeds of steers and two diets. Two commercially relevant beef breeds were used: Charolais-crossbreds (CHx; n=41) and purebred Luing steers (n=39). This design contrasted the fast-growing Charolais with the hardier Scottish Luing breed (a Beef Shorthorn x Highland Cattle composite). Two diets (as total mixed rations) were generated using a diet mixing wagon and consisted of forage to concentrate ratios (g/kg DM) of either

500:500 (Mixed: 12.0 MJ/kg DM; 500g/kg) or 79:921 (Concentrate: 12.8 MJ/kg DM; 920 g/kg). See Supplementary Table 1 and Duthie et al. (2017) for further details. The experimental design was reviewed and approved by SRUC's Animal Ethics Committee in accordance with UK Home Office guidelines.

2.1 Animals and Management

The steers were either homebred or purchased from Scottish farms and transported to the beef cattle research facility. In preparation for the trial, the steers were fed on a standard 50:50 forage:concentrate diet. They were transferred to 4 test pens at the start of the adaptation phase. These test pens were 18.4 x 9.9m. Feed was provided *ad libitum* from automatic feeders (HOKO, Insentec, Marknesse, The Netherlands), which recorded the start and stop weight of the feed alongside time of entry and exit from the individual feeder for each visit by each animal. Steers on the CONC diet were transitioned to the new concentrate levels gradually as part of the adaptation phase. There were 8 feeders per pen (2.5 animals/pen) and a water trough providing *ad libitum* access to water. Feed bins were refilled at approximately 8:00am each day. Each pen contained 20 animals and pens were balanced for breed and age, with starting weight balanced within breed. Animals were 3912 ± 3 days of age and 471 ± 62 kg bodyweight (BW) at the start of the experiment. Two pens were allocated to each of the 2 diets. Diets were fed in separate pens, as previous studies have shown that animals on less preferred diets could 'steal' feed from feed bins with the preferred diet which would bias the feed intake results (e.g. ; Ruuska et al., 2014; Tolkamp et al., 2000). This 'stealing' was noted in preliminary trials using this research facility, and subsequent studies have all used one feed per pen (e.g. Duthie et al., 2016; Llonch et al., in press). There is also a risk of acidosis in animals obtaining appreciable quantities

of a diet with a greater level of concentrate by stealing without an appropriate adaptation period.

There was a 4-week adaptation phase to allow the animals to adapt to the pens, the new social group and the automatic feeders, and to gradually introduce the test diets. The 56-day performance and feed efficiency testing phase started directly afterwards. Animals were weighed once a week on a calibrated weigh scale. Daily dry matter intake (DMI: kg/d) was recorded for each animal. Ultrasonic fat depth (FD) at the 12th/13th rib was taken for all steers at the end of the 56-day test period (see Duthie et al., 2017 for further details).

2.2 Behavioural Measures

Three major classes of behavioural variables were assessed: feeding behaviour, activity and dominance. These measures were all assessed during a performance test period, when feed efficiency and other traits were assessed.

Feeding behaviour was monitored automatically throughout the test period using the automatic feeders. Visits with negative intake values were excluded from the calculations. Feeding visits were not converted to meals, as suggested by Yeates et al. (2001), because this calculation allows short non-feeding intervals within an overall feeding period (or meal) to be identified and removed. However, an interval within a meal may be the result of an animal being displaced from the feeder by another animal. As the presence of these disruptions in feeding may be related to dominance rank, we wished to include these types of non-feeding intervals. Feeding data on days on which the animals were weighed (Mondays) were excluded, as time out of the pen would disturb normal feeding patterns. A number of parameters were calculated: mean number of feeding events/day (visits in which any quantity of feed was ingested:

nFeedVisit), total time spent feeding/day (FeedTime), average length of feeding visits (dFeedVisit) and standard deviation of the duration of the feed visits in a day (sdFeedVisit) as a measure of variability in the feeding visits. The daily fresh weight intake (Intake) was divided by FeedTime to calculate intake rate (IntakeRate).

Activity was assessed using activity monitors on Days 7 to 56 inclusive only due to limitations in data storage on the devices. Standing, lying, number of steps taken and summed overall motion was assessed using a tri-axial accelerometer-based activity monitor (IceTag Pro) and extracted from the device using IceManager 10 (IceRobotics, Queensferry, UK). An IceTag was attached to each animal above the fetlock joint. Lying bouts of less than 5 mins were eliminated as erroneous (as shown in Tolkamp et al., 2010). The amount of time spent standing/day (mins), the number of standing bouts, the average length of the standing bouts, the number of steps and the total motion index were extracted for each day. The motion index is absolute acceleration against gravity summed over the day, from which a step-count is derived. Any bout of behaviour that started before midnight and ended after midnight are not split across days, but are counted into the day in which it started. Weigh days and the first 3 days after initial tagging were excluded as not providing representative data (Mackay et al., 2012). The data were then summarised across all qualifying test days to give mean time standing/day (StandTime), mean number of standing bouts/day (nStandBout), mean duration of standing bouts (dStandBout), standard deviation of standing bout length (sdStandBout), mean number of steps/day (nSteps) and standard deviation of steps/day (sdSteps), mean daily motion index (MI) and standard deviation of motion index (sdMI). Battery failures meant that activity data was collected on 73 of the animals.

Dominance was assessed by analysing interactions at the feed bins. Although other work has shown that priority of access may vary according to the contested resource (e.g. Val-Laillet et al., 2008), priority of access to the feeders was considered the most relevant to feed efficiency. Two black and white CCTV infrared cameras were set up above the feeders in each pen. Animals were identified for video-recording purposes by unique numbers applied in spray-on stockmarker. The cameras were attached to a high storage capacity computer that used Geovision software to store and organise the digital video files (Version 8, Geovision Inc., Taipei, Taiwan). The view from the cameras allowed all interactions at the feeders to be observed. Previous research has shown that the majority of the aggressive interactions occur in the first two hours following fresh feed provision (MacKay et al., 2013). The first, third and fifth twenty-minute segments of video from the first two hours following feeding were analysed for one day per week for the first to fourth weeks of the performance recording period inclusive. The identity of any animal displacing another from the feeder (using a physical butt or push with the head or a threatening behavioural display) and the identity of the animal it displaced was recorded (see MacKay et al., 2013). Three observers analysed the video-recordings. Their observations were balanced across the four groups. To assess inter-observer reliability, each observer watched the same three 20min recordings and the count of displacements compared. The inter-observer reliability was 85%. The displacement index (DispIndex) was used as a measure of dominance and calculated as the no. of times the animal displaced another/(no. of times it displaced another + no. of times it was displaced) (Mendl et al., 1992; Galindo and Broom, 2000). There were no animals that had zero values.

2.3 Growth and efficiency traits

236 Details on the efficiency traits are shown in detail in Duthie et al. (2017).
237 Briefly, growth was modelled by linear regression of BW against test date, to describe
238 average daily gain (ADG), mid-test BW (BW) and mid-test metabolic BW
239 ($MBW = BW^{0.75}$). The dry matter contents of individual feed components were
240 determined on duplicate samples twice weekly. Dry matter intake (DMI) was
241 calculated by adjusting fresh weight values recorded by the automatic feeders with
242 these dry matter content values. Daily DMI values were used to calculate average DMI
243 over the 56-day period. Feed conversion ratio (FCR) was calculated as average DMI
244 per day (DMI kg/day)/ADG. Residual feed intake (RFI) was calculated as the deviation
245 of actual DMI (kg/day) from DMI predicted based on linear regression of actual DMI
246 on ADG, MBW and fat depth at the 12/13th rib as suggested by Basarab et al., 2003.
247 Conventionally, RFI is calculated on a breed and diet basis. However, an RFI value
248 calculated over the whole group allows the animals to be ranked, and their behaviour
249 patterns compared, even if the absolute value is not comparable to other studies.

250

251 *2.4 Statistical analysis*

252 All variables were checked for normality. Fresh weight intake had a non-normal
253 distribution, so was log-transformed.

254 There were two stages to the analysis. As it had been hypothesised that
255 dominance would affect efficiency only indirectly via effects on feeding behaviour, the
256 first step was to determine whether dominance affected feeding behaviour. This was
257 done using Linear Mixed Models with REML to allow the major fixed effects (breed
258 and diet) and random effects (pen) to be modelled. Each feeding behaviour variable
259 was tested as the dependent variable, with breed, diet and DispIndex fitted as fixed
260 effects. The random term had terms for both pen and animals nested within pens.

Pearson correlations were used to examine the relationships between the continuous variables and means examined for the categorical traits.

Secondly, Linear Mixed Models for ADG, FCR and RFI were run in which all feeding behaviour and activity variables, DispIndex, breed, diet and age were eligible as explanatory variables. Each explanatory variable was firstly tested alone as a univariate and became a candidate for the multivariable model if it had a P-value less than 0.2. The candidate variables were then added into a multivariate model in a forward-stepwise fashion, with the order of the variables determined by the Wald statistics. Candidate variables were kept in the model if they had significance levels of $P < 0.05$ (when all other explanatory variables in the models had been fitted). Akaike Information Criterion (AIC) values, as a measure of goodness-of-fit, were used to further guide the modelling process. Pearson correlations were used to examine the relationships between the continuous variables, and means used to determine the direction of effects for categorical variables. Feed intake and feed intake rate were not included in models for FCR and RFI to avoid circularity, as these are at least partly accounted for in the calculation of these measures. The random effect was pen and animal nested within pen. Genstat (Version 16: www.genstat.co.uk) was used for all analyses. The numerator (ndf) and denominator (ddf) degrees of freedom are presented, and F statistics. Note that the ddf may not be a whole number due to the presence of missing data.

Data from two animals were excluded from the dataset and the analysis as they had very poor growth rates, suggesting an underlying health issue.

3. Results

Means and standard errors for behaviours are shown in Table 1. Effects of breed and diet on behaviour are shown in Table 2.

3.1 Effects of diet and breed

Steers on the MIXED diet had higher dry matter intakes ($F=1786.91$; $ndf,ddf=1,1.9$; $P<0.001$), higher nFeedVisit values ($F=390.66$; $ndf,ddf=1,1.6$; $P=0.006$) and higher daily feeding times than on the CONC diet ($F=67.13$; $ndf,ddf=1,2$; $P=0.015$). The CHx steers had greater intake rates than the LuIng steers ($F=5.54$; $ndf,ddf=1,72.1$; $P=0.021$), but the LuIng steers had longer FeedTime values ($F=6.52$; $ndf,ddf=1,72.1$; $P=0.013$). Overall, there was no difference in intake, number of feeding visits or length of feeding visit between the breeds ($P>0.05$). However, there was a tendency for CHx steers to have higher variation in their length of feeding visits ($F=3.45$; $ndf,ddf=1,72.1$; $P=0.067$). CHx steers had higher DispIndex scores than LuIng steers ($F=15.28$; $ndf,ddf=1,76$; $P<0.001$). The CHx steers had higher BW at the mid-point of the trial than the LuIng steers ($F=30.94$; $ndf,ddf=1,73.9$; $P<0.001$; mean and sem: CHx=550.3 \pm 7.3 kg; LuIng=476.4 \pm 7.3 kg). However, there was no relationship between intake and mid-point BW ($r=0.11$, $P=0.34$). Effect of breed and diet on ADG, FCR and RFI is shown in Supplementary Table 2 (after Duthie et al., 2017).

3.2 Relationship between dominance and feeding behaviour

There were significant relationships between dominance and a number of aspects of feeding behaviour. Steers with higher DispIndex scores had higher DMI ($F=10.55$; $ndf,ddf=1,72.5$; $P=0.002$) and feeding rates ($F=7.96$; $ndf,ddf=1,72.1$; $P=0.006$). There was no relationship between DispIndex and the total time spent

feeding each day or the length or frequency of feeding bouts. However, there was a tendency for steers with higher DispIndex scores to have less variation in the duration of their feeding visits ($F=3.47$; $ndf,ddf=1,67.3$; $P=0.07$).

3.3 Univariate and multivariate models

The variables that showed associations with ADG, FCR and RFI in the univariate analysis with a P value of <0.2 are shown in Table 3. The final models are shown below with model R^2 values in brackets. Variance explained by addition of each variable to the model is shown in Supplementary Table 3.

ADG: $\mu + \text{Diet} + \text{LogIntake} + \text{nStandBout}$ (0.33)

FCR: $\mu + \text{AgeStartTest} + \text{nStandBout}$ (0.13)

RFI = $\mu + \text{diet} + \text{Breed.sdFeedVisit}$ (0.36)

3.3.1 ADG

Animals on the CONC diet had the highest ADG ($F=17.78$, $ndf,ddf=1,48.6$; $P<0.001$; $\text{mean}\pm\text{SEM}$ (kg/day) (CONC: 1.7 ± 0.3 ; MIXED: 1.5 ± 0.4). Steers with higher ADG had more standing bouts ($F=6.74$; $ndf,ddf=1,67.3$, $P=0.013$; $r=0.38$, $P<0.001$) and higher intakes ($F=15.16$, $ndf,ddf=1,67.7$; $P<0.001$). A number of variables were significant at the univariate level including breed and DispIndex, but they were not significant in the overall model (Table 3).

3.3.2 FCR

There was no effect of breed or diet on FCR ($P < 0.05$). Animals that were younger at the start of the trial had lower (more favourable) FCR values ($F = 6.70$, $\text{ndf,ddf} = 1,66.3$; $P = 0.011$; $r = 0.24$, $P = 0.04$). Steers that had more standing bouts had lower FCR values ($F = 5.06$, $\text{ndf,ddf} = 1,66.8$, $P = 0.028$; $r = -0.22$, $P = 0.06$)

3.3.3 RFI

There was an interaction between breed and variation in the length of the feeding event ($F = 9.71$, $\text{ndf,ddf} = 1,55.4$; $P = 0.003$) suggested that for the Luings, efficiency (low RFI values) was associated with low variation in the length of feeder visits ($r = 0.39$, $P = 0.02$). However, in the CHx steers, there was a tendency for the opposite association ($r = -0.28$, $P = 0.07$). There was an effect of diet in this model ($F = 26.02$, $\text{ndf,ddf} = 1,2.1$; $P = 0.032$) suggesting that steers were more efficient on the MIXED diet (RFI values = 0.28 vs -0.30 for CONC and MIXED diet respectively).

4. Discussion

In the present study, feed intake was affected by dominance, with steers with a greater ability to displace others achieving higher intakes. More dominant steers also tended to be heavier, and were more likely to be of the CHx breed. Fast-growing CHx steers have a higher growth potential than the hardier Luing steers and may simply have had a higher feed intake requirement. This would be a parsimonious explanation for the finding that the dominant animals had higher intakes. However, there was no relationship between liveweight and intake, which negates this explanation. The relationship between dominance and intake appears to be more than simply the effect of breed and weight, and it is likely to relate to other elements of the behaviour and temperament of the animals that were not assessed in this study. Ideally, a study would

be made with a single breed and diet, and more pens of animals, to provide further clarity on the effect of dominance per se, as we were not able to do in this experiment. However, the mixed breeds, and sometimes diets, used in this study is typical of those used in other feed efficiency trials (e.g. Basarab et al., 2003; Durunna et al. 2011; Fitzsimons et al., 2014; Llonch et al., in press).

This finding has potential implications for studies in which the growth rate of animals is assessed. If animals are tested in situations where there is not full access to feed simultaneously for all animals, low ranking animals may not achieve their full growth potential. Similar studies in situations where group-housed animals are fed from a limited number of bins have also shown that low-ranking animals have poorer access to feed (McPhee et al., 1964; Stricklin and Gonyou, 1981) and lower weight gains (Brouns and Edwards, 1994). However, most recent studies in cattle have shown that despite dominant animals having greater access to the feeders, no difference was found in total daily intake between dominant and subordinate, or younger and older animals (beef cattle: Stricklin and Gonyou, 1981; dairy cattle: Hosseinkhani et al., 2008; Proudfoot et al., 2009; Collings et al., 2011). The variation in results across these studies suggest that the levels of displacement and its subsequent impact on feed intake are likely to be related to the space allowance at the feeders and also to the feeding motivation of the animals. The studies in dairy cattle mentioned above all had a bin:cow ratio of 1:2 in the ‘competitive’ situation and 1:1 in the ‘non-competitive’ situation. The present study had a higher ratio of approximately 1:2.5, which may explain the greater impact on feed intake. Many studies investigating RFI in beef cattle had similar or higher bin:animal ratios (e.g. Golden et al., 2008: 1:5; Lancaster et al., 2009: 1:6-8).

The average FeedTime per animal in this study was 133.4 mins/day. With an average of 2.5 animals/bin this means that each bin may have only been occupied for 5.5h/day. This suggests that there was no real time constraint on access to the feeder, and yet observations of high levels of interactions at the feeder in this and similar studies in the period just after food delivery suggest that steers are strongly motivated to access the feeder when fresh feed is delivered (e.g. Mackay et al., 2013). There are a number of reasons for this. Fresh feed may be attractive to cattle and the bins may be easier to feed from when they are full. Cattle are also a social species, and are motivated to feed together (e.g. O'Connell et al., 1989), providing further motivation for animals to join the influx of animals to the feeders when feed is first delivered. Dairy cattle have also been shown to 'sort' fresh feed to preferentially select the larger concentrate particles of the feed (De Vries et al., 2008). It is possible that beef cattle on mixed rations in studies such as this one may also sort feed, which means that the quality of the ration declines over the day.

Feeding rate was also influenced by dominance, with higher intake rates shown by steers of higher DispIndex scores. In other studies with dairy cattle, increased feeding rates have been shown in situations of competition compared to non-competitive situations (Hosseinkhani et al., 2008; Collings et al., 2011), and so it might have been expected that intake rate would be higher in subordinate animals. As suggested above, there was no real time restriction on feeding time, and so no need for subordinate animals to eat faster. Additionally, as it was the larger animals that had the higher DispIndex scores, their greater size may have allowed them to eat faster. The indication of a slightly lower variation in feeding visit length for dominant animals suggests that these animals were being disturbed less by other animals or events

408 compared to subordinate animals. This greater consistency in feeding visit length in
409 dominant animals has been shown elsewhere (e.g. Post et al., 1980).

410 Despite DispIndex showing a weak association with ADG and being a candidate
411 variable for the full model of ADG (Table 2), DispIndex did not appear in the final
412 model. This suggests that subordinate animals are still able to access sufficient feed to
413 support growth. However, ADG was affected by intake, so there may be an indirect
414 effect of dominance on ADG through its association with intake. Additionally,
415 DispIndex was not associated with FCR or RFI. However, the lower feed intake seen
416 in subordinate animals suggests that these animals are not able to fully express their
417 potential for growth or efficiency. This may be the case in studies in which there is less
418 than a 1:1 ratio between feeders and animals, or sufficient space at an open feed-trough
419 for all animals to feed simultaneously. It is probable that ADG values, and possibly
420 also FCR and RFI measures, for subordinate animals will depend on the level of access
421 to feed. Additionally, it means that FCR values may not be comparable across studies,
422 as the level of feed competition imposed in the trial may affect recorded values. This
423 argument is not relevant for RFI values, as RFI values are a ranking of animals relative
424 to the group mean.

425 Genetic selection for highly efficient animals is seen as an important way of
426 improving the overall efficiency of beef production (Archer et al., 1999; Robinson and
427 Oddy, 2004). Although there is no direct effect of dominance on efficiency, the use of
428 feed intakes in any genetic selection programme may be inadvertently selecting for
429 increased aggression in animals. Selection for productivity traits in isolation has been
430 shown to have adverse effects on animal health and welfare (Rauw, 1998), and there
431 may also be an issue in this situation. In practical terms, however, increasing access to

feed by increasing the length of feed trough per animal may improve intake and ADG for all animals in the group.

It has been found previously that higher activity is associated with poorer efficiency in beef cattle (Herd et al., 2004, Llonch et al., (in press)) as shown by the number of steps taken. No relationship between efficiency and activity, expressed in the step count, MI and total standing time, was found in the present study. The results show that there was an association between lower (better) FCR values and a higher number of standing bouts. Animals may be standing to access feed and water, or to perform other behaviours as required, in short bouts, with no overall effect on standing time. Steers with lower RFI scores also had more consistent lengths of standing bouts. This consistency suggests that the animal is able to voluntarily choose the length of standing bout, rather than it being influenced by other animals or the husbandry procedures. In group housing situations, where animals must walk to get feed and water, and interactions with other animals are likely to be frequent, all animals must be reasonably active, and distinguishing between active and inactive genotypes is difficult. Additionally, there has likely been direct or indirect selection against animals that are over-reactive to group housing, also reducing the likelihood of there being an overt influence of activity on efficiency.

Overall, some associations between feeding behaviour and efficiency were evident in the modelling of factors affecting FCR and RFI, contrary to what has been shown in other studies (Basarab et al., 2007; Nkrumah et al., 2007a; Golden et al, 2008; Lancaster et al 2009; Kelly et al., 2010; Durunna et al., 2011). Low variation in the length of the feeder visits was associated with lower RFI values for the Luing steers. A consistent length of feeder visits suggests that these animals maintained a consistent feeding strategy across days or were not disturbed during feeding. This strategy clearly

allowed these animals to maximise feed efficiency and also corresponds to the relationship between consistency of standing bouts and efficiency. However, there was a non-significant association in the opposite direction for the CHx steers, suggesting that the most effective feeding strategies depend on the animal and the situation. Relationships between feeding traits and RFI are typically analysed by dividing animals into groups (e.g. low and high, or low, medium and high) and modelling the effect of feeding traits (e.g. Golden et al., 2008; Fitzsimons et al., 2014) rather than using individual animal RFI value as a continuous trait in a model which considered all possible influencing factors. The results of this study suggest that individual animal characteristics affect feed intake and feeding behaviour, which suggests that RFI and other traits should be modelled as continuous traits that allow these characteristics to be taken into account. Further confirmation is needed, but these results suggest that individual animals adopt particular behavioural strategies dependent upon their genotype and diet. The concept that animals will adapt their feeding behaviour and activity in response to the social context and resource availability, and that this may affect their growth and efficiency is not considered in the field of feed efficiency in beef cattle. By providing more feeder space per animal and/or lower stocking density, overall efficiency in groups of animals may be improved.

5. Conclusion

In conclusion, the results suggest that feed intake and feeding rate were affected by dominance rank in the experimental conditions that are typically used to estimate feed efficiency. This may indirectly affect ADG at the level of the individual animal. While dominance did not directly affect RFI or FCR, the results suggest that situations in which animals must compete for feed may impair their ability to achieve optimal

growth. Behavioural traits influence efficiency as efficient animals have more consistent standing bout and feeder visit lengths.

Conflicts of interest

The authors declare that they have no conflicts of interest

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References

- Archer, J.A., Richardson, E.C., Herd, R.M., Arthur, P.F., 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. *Aust. J. Agric. Res.* 50, 147-161.
- Arthur, P.F., Archer, J.A., Herd, R.M., 2004. Feed intake and efficiency in beef cattle: overview of recent Australian research and challenges for the future. *Aust. J. Exp. Agric.* 44, 361-369.
- Basarab, J.A., Price, M.A., Aalhus, J.L., Okine, E.K., Snelling, W.M., Lyle, K.L., 2003. Residual feed intake and body composition in young growing cattle. *Can. J. Anim. Sci.* 83, 189-204.

- Basarab, J.A., McCartney, D., Okine, E.K., Baron, V.S., 2007. Relationships between progeny residual feed intake and dam productivity traits. *Can. J. Anim. Sci.* 87, 489–502.
- Brouns, F. and Edwards, S.A., 1994. Social rank and feeding behaviour of group-housed sows fed competitively or ad libitum. *Appl. Anim. Behav. Sci.* 39, 225-235.
- Collings, L.K.M., Weary, D.M., Chapinal, N., von Keyserlingk, M.A.G., 2011. Temporal feed restriction and overstocking increase competition for feed by dairy cattle. *J. Dairy Sci.* 94, 5480–5486.
- DeVries, T.J., Dohme, F., Beauchemin, K.A., 2008. Repeated ruminal acidosis challenges in lactating dairy cows at high and low risk for developing acidosis: feed sorting. *J. Dairy Sci.* 91, 3958–3967.
- Durunna, O.N., Wang, Z., Basarab, J.A., Okine, E.K., Moore, S.S., 2011. Phenotypic and genetic relationships among feeding behaviour traits, feed intake, and residual feed intake in steers fed grower and finisher diets. *J. Anim. Sci.* 89, :3401-3409.
- Duthie, C-A., Rooke, J. A. Troy S., Hyslop, J. J. Ross, D. W. Waterhouse, A., Roehe R., 2016. Impact of adding nitrate or increasing the lipid content of two contrasting diets on blood methaemoglobin and performance of two breeds of finishing beef steers. *Animal* 10, 786-795.
- Duthie, C-A., Haskell, M.J., Hyslop, J.J., Waterhouse, A., Wallace, R.J., Roehe, R., Rooke, J.A., 2017. Breed and diet of finishing beef steers have different effects on performance, methane emissions and rumen characteristics. *Animal*. 11, 1762-1771.
- Fitzsimons, C., Kenny, D. A., Fahey, A.G., McGee, M., 2014. Feeding behaviour, ruminal fermentation, and performance of pregnant beef cows differing in phenotypic residual feed intake offered grass silage. *J. Anim. Sci.* 92, 2170-2181.
- Galindo, F. and Broom, D.M., 2000. The relationships between social behaviour of dairy cows and the occurrence of lameness in three herds. *Res. Vet. Sci.* 69, 75-79.
- Gibbons, J.M., Lawrence, A.B., Haskell, M.J., 2009. Consistency of aggressive feeding behaviour in dairy cows. *Appl. Anim. Behav. Sci.* 121, 1-7.
- Golden, J.W., Kerley, M.S., Kolath, W.H., 2008. The relationship of feeding behaviour to residual feed intake in crossbred Angus steers fed traditional and no-roughage diets. *J. Anim. Sci.* 86, 180-186.
- Hafla, A.N., Carstens, G.E., Forbes, T.D.A., Tedeschi, L.O., Bailey, J.C., Walter, J.T., Johnson, J.R., 2013. Relationships between postweaning residual feed intake in heifers and forage use, body composition, feeding behaviour, physical activity, and heart rate of pregnant beef females. *J. Anim. Sci.* 91, 5353-5365.

- Herd, R.M., Oddy, V.H., Richardson, E.C., 2004. Biological basis for variation in residual feed intake in beef cattle. 1. Review of potential mechanisms. *Aust. J. Exp. Agric.* 44, 423-430.
- Hosseinkhani, A., DeVries T.J., Proudfoot, K.L., Valizadeh, R., Veira, D.M., Keyserlingk, M.A.G., 2008. The effects of feed bunk competition on the feed sorting behavior of close-up dry cows. *J. Dairy Sci.*, 91, 1115–1121.
- Huzzey, J.M., DeVries T.J., Valois, P., von Keyserlingk, M.A.G., 2006. Stocking density and feed barrier design affect the feeding and social behavior of dairy cattle . *J. Dairy Sci.* 89, 126–133.
- Hyslop, J.J., Duthie, C-A., Ross, D.W., Rooke, J.A., Roehe, R., 2012. An assessment of alternative test length periods when measuring liveweight change in finishing cattle during feed efficiency studies. *Proceedings of the British Society of Animal Science and the Association of Veterinary Teaching and Research Work*, April 2012, Vol 3; Part 1. Paper 46.
- Kelly, A.K., McGee, M., Crews, D.H. Jr., Fahey, A.G., Wylie, A.R., Kenny, D.A., 2010. Effect of divergence in residual feed intake on feeding behaviour, blood metabolic variables, and body composition traits in growing beef heifers. *J. Anim. Sci.* 88, 109-123.
- Koch, R.M., Swiger, L.A., Chambers, D., Gregory, K.E., 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* 22, 486-494.
- Lancaster, P.A., Carstens, G.E., Ribeiro, F.R.B., Tedeschi, L.O., Crews, D.H., Jr., 2009. Characterization of feed efficiency traits and relationships with feeding behaviour and ultrasound carcass traits in growing bulls. *J. Anim. Sci.* 87, 1528-1539.
- Lawrence, P., Kenny, D.A., Earley, B., Crews, D.H., Jr., McGee, M., 2011. Grass silage intake, rumen and blood variables, ultrasonic and body measurements, feeding behaviour, and activity in pregnant beef heifers differing in phenotypic residual feed intake. *J. Anim. Sci.* 89, 3248-3261.
- Llonch P., Somarriba, M., Duthie, C.A., Troy, S., Roehe R., Rooke, J.A., Haskell M. J., Turner, S. P. (in press). Temperament and dominance relate to feeding behaviour and activity in beef cattle: implications for performance and methane emissions. *Animal*.
- Luiting, P., Urff, E.M., Verstegen, M.W.A., 1994. Between-animal variation in biological efficiency as related to residual feed consumption. *Neth. J. Agric Sci.* 42, 59-67.
- MacKay, J.R.D., Deag, J.M., Haskell, M.J., 2012. Establishing the extent of behavioural reactions in dairy cattle to a leg mounted activity monitor. *Appl. Anim. Behav. Sci.* 139, 35-41.

- MacKay, J.R.D., Turner, S.P., Hyslop, J., Deag, J. M., Haskell, M. J., 2013. Short term temperament tests in beef cattle relate to long term measures of behaviour recorded in the home pen. *J. Anim. Sci.* 91, 4917-4924.
- McPhee, C.P. McBride, G., James, J.W., 1964. Social behaviour of domestic animals III. Steers in small yards. *Anim. Sci.* 6, 9-15.
- Mendl, M., Zanella, A. J., Broom, D. M., 1992. Physiological and reproductive correlates of behavioural strategies in female domestic pigs. *Anim. Behav.* 44, 1107–1121.
- Nkrumah, J.D., Crews, D.H., Jr, Basarab, J.A., Price, M.A., Okine, E.K., Wang, Z., Li, C., Moore, S.S., 2007. Genetic and phenotypic relationships of feeding behaviour and temperament with performance, feed efficiency, ultrasound and carcass merit of beef cattle. *J. Anim. Sci.* 85, 2382-2390.
- O'Connell, J., Giller, P., Meaney, W., 1989. A Comparison of Dairy Cattle Behavioural Patterns at Pasture and during Confinement. *Irish. J. Agric.Res.* 28, 65-72
- Post D.G., Hausfater G., McCuskey, S.A., 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): Relationship to age, gender and dominance rank. *Folia Primatol.* 34, 170–195.
- Proudfoot, K.L., Veira, D.M., Weary, D.M., von Keyserlingk, M.A.G., 2009. Competition at the feed bunk changes the feeding, standing and social behavior of transition dairy cows. *J. Dairy Sci.* 92, 3116-3123.
- Rauw, W.M., Kanis, E., Noordhuizen-Stassen, E.N., Grommers, F.J., 1998. Undesirable side effects of selection for high production efficiency in farm animals: a review. *Livest. Prod. Sci.* 56, 15-33.
- Robinson, D.L. and Oddy, V.H., 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. *Livest. Sci.* 90, 255–270.
- Richardson, E.C., Herd, R.M., Colditz, I.G., Archer, J.A., Arthur, P.F., 2002. Blood cell profiles of steer progeny from parents selected for and against residual feed intake. *Aust. J. Exp. Agric.* 42, 901-908.
- Richardson, E.C., Herd, R.M., Oddy, V.H., 2000. Variation in body composition, activity and other physiological processes and their associations with feed efficiency. In 'Feed efficiency in beef cattle. Proceedings of the Feed Efficiency Workshop'. Eds: J.A. Archer, R.M. Herd and P.F. Arthur, pp 46-50. University of New England, Armidale, NSW.
- Ruuska, S., Hämäläinen, W., Sairanen, A., Juutinen, E., Tuomisto, L., Järvinen, M., Mononen, J., 2014. Can stealing cows distort the results of feeding trials? An experiment for quantification and prevention of stealing feed by dairy cows from roughage intake control feeders. *Appl. Anim. Behav. Sci.* 159, 1-8.

- Stricklin, W.R. and Gonyou, H.W., 1981. Dominance and eating behavior of beef cattle fed from a single stall. *Appl. Anim. Ethol.* 7, 135-140.
- Syme, G.J., 1974. Competitive orders as measures of social dominance. *Anim. Behav.* 22, 931-940.
- Tolkamp, B.J., Schweitzer, D.P.N., Kyriazakis, I., 2000. The biologically relevant unit for the analysis of short-term feeding behaviour of dairy cows. *J. Dairy Sci.* 83, 2057-2068.
- Tolkamp, B.J., Haskell, M.J., Langford, F.M., Roberts, D.J., Morgan, C.A., 2010. Are cows more likely to lie down the longer they stand? *Appl. Anim. Behav. Sci.* 124, 1-10.
- Val-Laillet, D., Viera, D.M., Von Keyserlingk, M.A.G., 2008. Short communication: dominance in free-stall-housed dairy cattle is dependent upon resource. *J. Dairy Sci.* 91, 3922-3926
- Yeates, M.P., Tolkamp, B.J., Allcroft, D.J., Kyriazakis, I., 2001. The use of mixed distribution models to determine bout criteria for analysis of animal behaviour. *J. Theor. Biol.* 213, 413-425.